

MORTALITY AND AGE OF BLACK COTTONWOOD STANDS ALONG DIVERTED AND UNDIVERTED STREAMS IN THE EASTERN SIERRA NEVADA, CALIFORNIA

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ABSTRACT

Effects of stream flow diversion on riparian vegetation can range from extreme to subtle. Extreme effects include extensive loss of riparian vegetation, such as has occurred along portions of Bishop Creek, Rush Creek, and other eastern Sierra Nevada streams diverted for hydropower production and municipal water use. Some diverted reaches of these and other streams, however, have relatively dense vegetation. This study revealed the presence of subtle diversion effects within such reaches of Bishop Creek, as indicated by younger age and size, higher mortality, and lower canopy foliage density of black cottonwood stands (*Populus trichocarpa*) in comparison to black cottonwood stands along a nearby free-flowing river (Pine Creek). Tree ring analysis implicated chronic drought and episodic floods as causes of this reduced biotic integrity. Droughts have become more frequent and intense, as a result of greater flow diversion during dry and normal years than in wet years. The frequency of flood flows has been diminished, but the magnitude of rare extreme flood events has been little affected. Restoration of biotic integrity depends, in part, on restoration of minimum and maximum flows that approximate natural conditions.

Damming of rivers for hydropower production, flood control, or water supply often results in substantial change in the downstream flow regime (Chien 1985). Annual flow volume may be reduced; seasonal flow peaks may shift from spring to summer if flows are released after reservoir filling; and annual fluctuation in flow volume may increase if flow diversion is greater during dry and normal years than in wet years. The effects of these changes on downstream riparian vegetation range from extreme to subtle (Williams and Wolman 1984; Risser and Harris 1989). The extreme effects, notably widespread loss of low elevation riparian ecosystems, have stimulated research on restoration and maintenance of endangered riparian ecosystems, including development of instream flow methodologies for riparian vegetation (Stromberg and Patten 1990). The less apparent subtle changes have engendered controversy over the effects of stream diversion while also stimulating research on identification of streams that are least sensitive to diversion (Kondolf et al. 1987).

Within California, the riparian ecosystems of the eastern Sierra Nevada have been extensively managed for their water resources.

At Bishop Creek, for example, streamflow has been diverted for hydropower production for nearly a century (Stromberg and Patten 1991). This has reduced the extent of riparian vegetation in many stream reaches. Out-of-basin flow diversion for municipal use at Rush Creek similarly has caused loss of riparian vegetation (Stine et al. 1984; Stromberg and Patten 1990). As is true for many diverted streams, however, some diverted reaches on both Bishop and Rush creeks support stands of cottonwoods (*Populus* spp.) and other riparian vegetation. The mere presence of riparian trees, though, cannot be used as the sole indicator that flow regimes are providing for a high degree of biological integrity (Karr 1991). Although ecosystem level changes indicative of extreme stress may not be present (e.g., changes in species composition), there may be population level changes indicative of a lower level of stress (Taub 1987). For example, riparian cottonwood populations may recruit infrequently or have high mortality as a result of altered flow pattern or reduced flow volume. Recruitment is particularly sensitive to flow conditions, and often depends on a particular sequence of flows such as high spring flows followed by reduced summer flooding (Stromberg et al. 1991). Mortality in riparian systems also is strongly influenced by flow regimes. Flood flows and low flows alike are primary causes of mortality, particularly for juvenile and senescent trees (Albertson and Weaver 1945; McBride and Strahan 1984; Hunter et al. 1987; Smith et al. 1991). Thus, parameters indicative of biotic integrity, such as population age structure and mortality, should be assessed along diverted and regulated streams (Karr 1991).

Studies of vegetational parameters such as age structure and mortality can be useful in understanding ecological processes and thereby avoiding adverse environmental impacts (Franklin et al. 1987). Within riparian ecosystems, for example, if tree mortality is found to be caused by a particular flow regime, this information can be useful in prescribing appropriate instream flows for managing riparian vegetation. This study was undertaken with the primary objective of comparing: (1) vegetation structure; (2) black cottonwood (*P. trichocarpa*) size and age structure, including maximum tree size and age; and (3) extent and causes of mortality for mature black cottonwood; between a partially diverted stream (Bishop Creek) and a nearby free-flowing stream (Pine Creek) in the eastern Sierra Nevada of California. A secondary objective was to identify flow regimes associated with mortality of black cottonwood along diverted Rush Creek, also in the Sierra Nevada. Such information is important because of the rarity and value of riparian cottonwood ecosystems in the American West, and because of the utility of the data in helping to define appropriate flow regimes for riparian ecosystem maintenance.

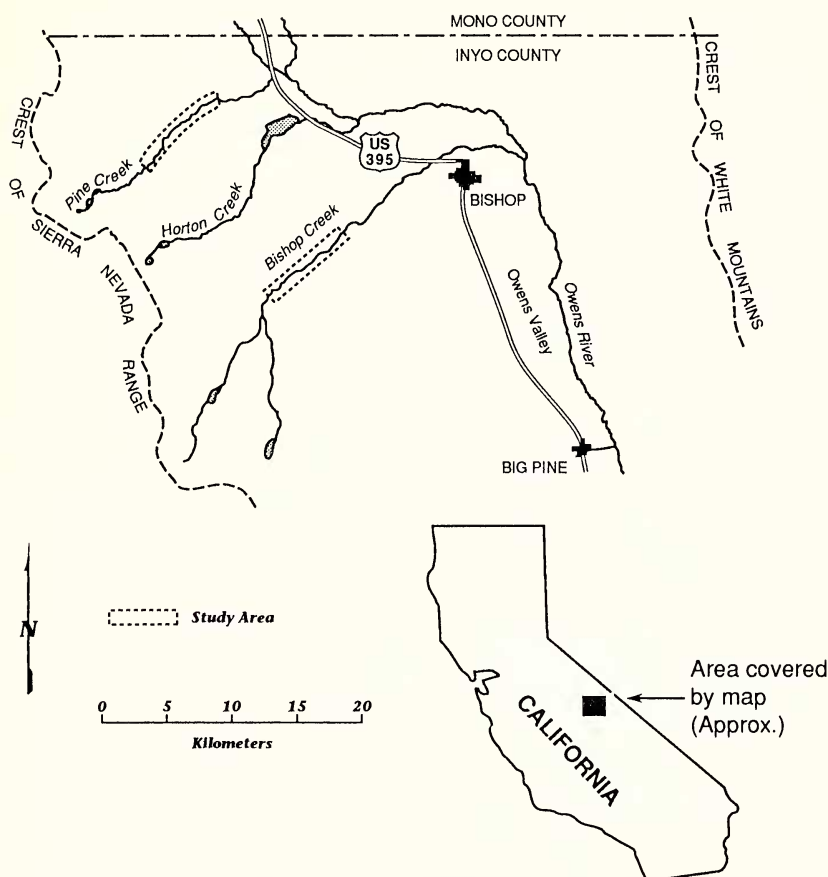


FIG. 1. Location map for study areas along Bishop and Pine creeks. The Rush Creek study area is located about 75 km north of Pine Creek within the Mono Basin.

STUDY AREAS

Bishop Creek drains a 180 km² watershed in the rainshadow of the eastern Sierra Nevada (Fig. 1). In its upper reaches, Bishop Creek flows over bedrock and glacial till through steep alpine and coniferous landscapes in a glacially carved canyon. The stream in its mid and lower reaches is surrounded by Great Basin shrub desert and flows over an alluvial fan before entering the Owens River Valley. Riparian vegetation in the mid-elevation reaches (ca. 1500–2000 m) is dominated by black cottonwood, water birch (*Betula occidentalis*), willow (*Salix* spp.), Jeffrey pine (*Pinus jeffreyi*), and mountain rose (*Rosa woodsii ultramontana*). Vegetation cover decreases with elevation, and black cottonwood gradually gives way to Fremont cottonwood (*Populus fremontii*) hybrids at about 1500 m.

Five hydroelectric power plants operate on Bishop Creek. In dry and normal snow pack years, all of the water is diverted from the channel into a series of pipelines and reservoirs, and used to generate power. At these times, any water present in the stream arises from dam leakage and/or groundwater input; often no surface flow is present in the lower reaches. In wet years, snowmelt delivers water at a rate that exceeds the capacity of the facilities and the excess flow spills into the stream. At each power plant a small intake dam collects the water exiting the plant plus any flows in the stream. The dam delivers the water to the next power plant through another pipeline. Flows are ultimately released into the stream channel below the lowermost power plant.

Pine Creek is a free-flowing stream located 15 km north of Bishop Creek (Fig. 1). The stream drains a 98 km² watershed and flows over deep sedimentary fill through a glacially carved U-shaped valley (Kondolf et al. 1987). In its mid-elevation reaches (1500–2000 m), Pine Creek is dominated by water birch and black cottonwood, with a shrub understory of mountain rose. Fremont cottonwood is present at low elevations, but in a landscape highly modified by ranching activities.

Rush Creek is the largest tributary to Mono Lake. It flows from the eastern slope of the Sierra Nevada through a narrow mountain valley until it is impounded in Grant Lake Reservoir, from which water is diverted to the City of Los Angeles. Diversion was limited during the first few years after construction of the reservoir (1942), but from 1948 on releases were minimal except in wet years. The riparian vegetation below Grant Lake is dominated by black cottonwood, several species of willow, and Jeffrey pine.

METHODS

Our research approach included assessment of: (1) vegetation structure; (2) black cottonwood size and age structure; and (3) extent and causes of mortality for mature cottonwood trees. The first parameters were measured in each of three diverted reaches of Bishop Creek and three elevationally matched reaches of Pine Creek. The second parameters were measured for these same reaches and for an additional high-elevation diverted reach of Bishop Creek. The third parameters were determined for one reach of Bishop Creek with high mortality, and for a diverted reach of Rush Creek at ca. 2000 m. The Bishop creek reaches range in elevation from 2380 m (reach 1) to 1470 m (reach 4) and are numbered based on the number of the nearest upstream powerplant. Numbers of Pine Creek reaches (2, 3 and 4) correspond to numbers of elevationally matched Bishop Creek reaches.

Vegetation structure. Vegetation structure was assessed by measuring canopy foliage density (i.e., leaf area index) and by identifying the dominant woody plants. Canopy foliage density was measured in 1991, by sampling fifty points per reach with a LICOR 2000 plant canopy analyzer. Measurements were taken in early morning or under shaded sky conditions to minimize error (Welles 1990). Canopy foliage densities were compared between elevationally matched reaches of Pine and Bishop creeks using Student's t-tests. To identify dominant woody species, woody plant density by species was sampled within four, 10 m \times 50 m quadrats per reach. Species names follow Munz and Keck (1973).

Size and age structure. Black cottonwood size structures were generated based on stem diameters measured in four, 10 m \times 50 m quadrats per reach. To generate age structure, increment cores (two per tree) and stem diameters were taken for 14 to 50 trees per reach. After cross-dating the increment cores, the trees were aged by counting the number of growth rings and adding the estimated number of years to grow to the 1.5 m coring height (2 years at low elevations, 3 years at high elevations). Prior studies have indicated that black cottonwoods produce one growth ring per year (Stromberg and Patten 1990). Linear regression equations relating tree age to tree diameter were then developed with SPSS/PC+. These reach-specific equations were used to estimate ages of all trees measured for stem diameter.

Mortality. Mortality was calculated in 1989 as the percentage of standing dead or downed trees among the population of mature trees (those >10-cm dbh). Sample size for the mortality count was 100 trees, except in reaches with very small cottonwood populations. At this time, 15 to 50 live trees per reach were marked. The sites were revisited in Fall 1991 (during the fifth year of a drought) to assess mortality among the marked population of trees. To determine causes of past tree death, increment cores (two per tree) were collected from 10 randomly selected mature, dead black cottonwoods at Bishop Creek reach 2 and from 15 dead black cottonwood trees at Rush Creek. Dead trees were not cored at Pine Creek because there were few trees that had died from unknown causes. The diameter of each cored tree was measured, and the cores were mounted and sanded following standard procedures (Fritts and Swetnam 1989). Because of cellular decomposition, only 11 trees per stream had interpretable annual rings. The annual ring widths of these trees were measured with a Bannister type incremental measuring machine and standardized to remove age-related growth trends. To identify the year of death, the ring chronologies were cross-dated against reach chronologies developed previously for live trees (Stromberg and Patten

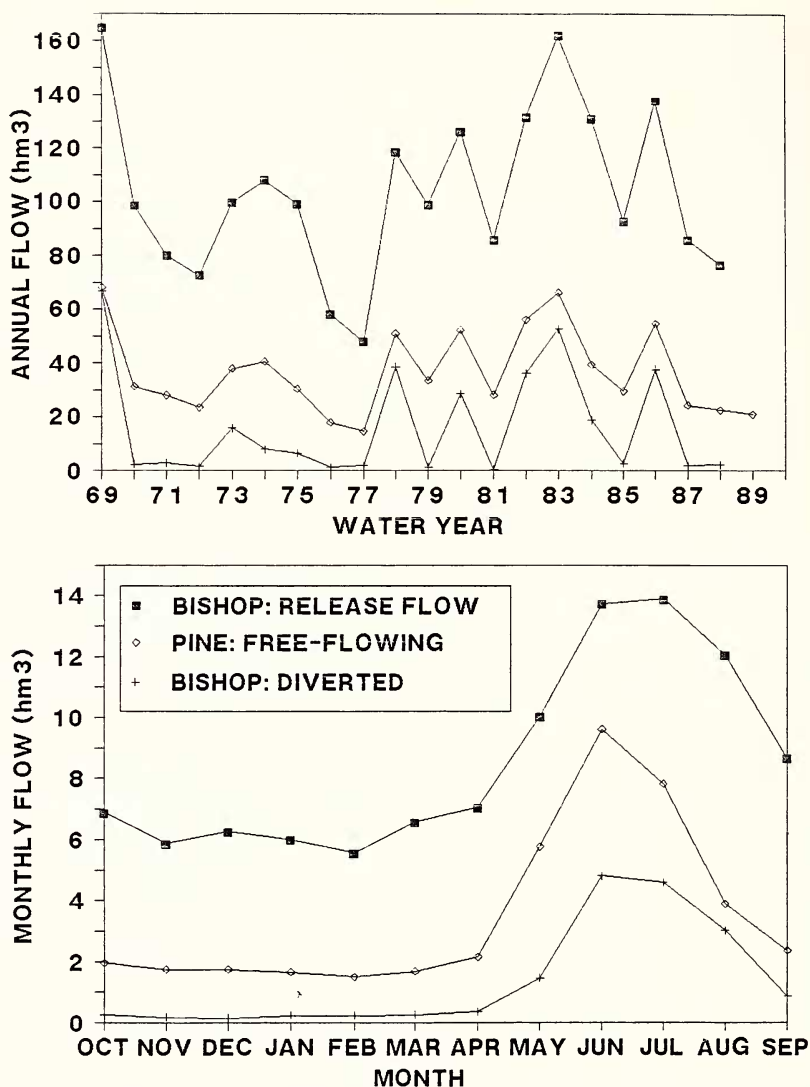


FIG. 2. Annual and monthly flow volume in free-flowing Pine Creek (1580 m), in a diverted reach of Bishop Creek (1390 m), and in the reach of Bishop Creek that receives the return flows (1380 m).

1990, 1991). Flow volume during the year of death was determined from data supplied by Southern California Edison Co. (Bishop Creek) and by Los Angeles Department of Water and Power (Rush Creek). The chronologies of the dead trees were also measured for annual growth rate and for mean sensitivity, an indicator of the degree of annual growth fluctuation (Fritts and Swetnam 1989). Growth rates and mean sensitivities were also measured for live trees within each

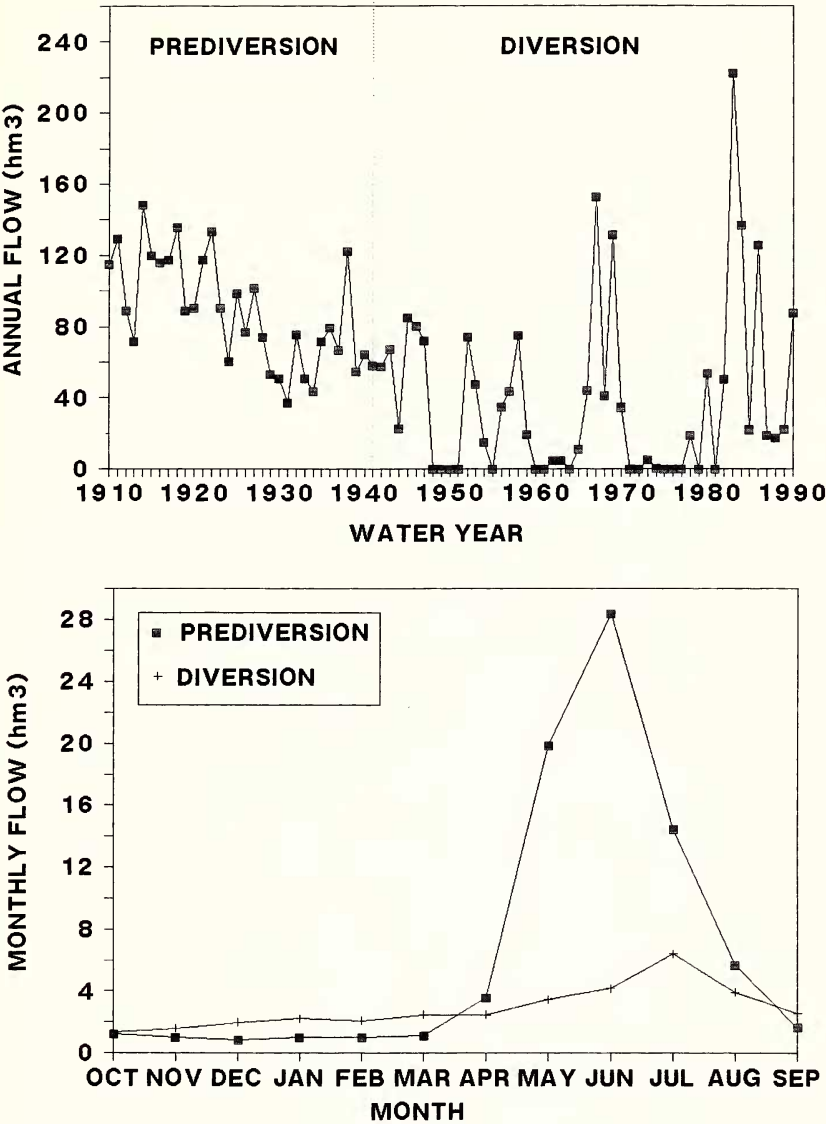


FIG. 3. Annual and monthly flow volume at Rush Creek (2180 m) during prediversion and diversion (post-1941) periods.

reach. Student's t-tests were used to compare values between live and dead trees, and between live trees on Bishop and Pine creeks.

RESULTS

Flow patterns. The diverted reaches of Bishop Creek have had extended periods of low flow punctuated by flood years (Fig. 2).

TABLE 1. STAND CANOPY FOLIAGE DENSITY, MORTALITY, DENSITY, AND ANNUAL VARIATION IN GROWTH RATE FOR *POPULUS TRICHOCARPA* AT DIVERTED BISHOP CREEK AND FREE-FLOWING PINE CREEK REACHES. Values are means \pm standard deviations.

Reach	Elev. (m)	Canopy foliage density ¹	Tree mortal- ity ² (%)	Tree density (no. 0.1 ha ⁻¹)	Juvenile density ³ (no. 0.1 ha ⁻¹)	Annual growth variation ⁴
Bishop 2	2020	1.73 \pm 0.16	27	28	98	35 \pm 13
Bishop 3	1800	0.51 \pm 0.12	14	33	93	39 \pm 14
Bishop 4	1470	0.35 \pm 0.12	33	6	42	49 \pm 29
Pine 2	2100	2.52 \pm 0.25	9	41	199	30 \pm 11
Pine 3	1850	2.14 \pm 0.19	0	45	170	24 \pm 09
Pine 4	1580	3.13 \pm 0.37	11	38	125	22 \pm 05

¹ Leaf area index (m² m⁻²).

² Dead trees as a percent of the total.

³ Juveniles are plants <10-cm stem diameter.

⁴ Mean sensitivity of the ring chronologies.

Flow volume ranged annually from <1 to >50 hm³ (in 1983), with an annual coefficient of variation of 116% to 139% among reaches. Instantaneous flows were very high in 1982 (>40 m³ s⁻¹), exceeding the 100-year flood rate. Average annual flow volume in the diverted reaches ranged from 9 hm³ at 2020 m to 16 hm³ at 1390 m, and was considerably lower than in the return flow reach (76 hm³ at 1380 m). Average annual flow volume in Pine Creek (50 hm³ at 1580 m) was intermediate between that in the diverted and return flow reaches of Bishop Creek. Pine Creek flows ranged annually from 24 to 83 hm³, but on average were more constant than at Bishop Creek (coefficient of variation in annual flow volume of 41%). Seasonal flow patterns in Pine Creek and the diverted Bishop Creek reaches showed the spring (June) peak characteristic of snowmelt fed eastern Sierra Nevada streams.

Annual flows in Rush Creek were considerably more erratic during the diversion period than the prediversion period (Fig. 3). Flows during the diversion period were characterized by extended periods of low or no flow during drought years to >221 hm³ (180,000 acre-feet) per year. Flows in recent years have been relatively high as a result of court orders requiring sufficient flows to maintain the stream's fisheries. Seasonal flow peaks at Rush Creek shifted from June (prediversion) to July (diversion period).

Vegetation structure. Canopy foliage density differed significantly between all three elevationally matched reaches of Bishop and Pine creeks ($P < 0.01$) (Table 1). The difference was most pronounced at low elevation reach 4, where values were 0.35 ± 0.12 for Bishop Creek and 3.13 ± 0.37 for Pine Creek. Black cottonwood density also was lower at Bishop Creek reaches, particularly at reach 4. Reach 4 at Pine Creek was dominated by black cottonwood, water birch,

and mountain rose. Reach 4 at Bishop Creek was dominated by these same species as well as by several upland species: *Purshia tridentata*, *Artemisia tridentata*, and *Chrysothamnus nauseosus*. Mid and upper reaches Bishop and Pine creeks supported similar species: black cottonwood, water birch, mountain rose, *Shepherdia argentea*, and various willow species (e.g., *Salix lasiolepis* and *Salix lasiandra*). Jeffrey pine was present within all Bishop Creek reaches.

Size and age structure. Age of black cottonwood could be predicted from stem diameter with only a moderate degree of confidence (Figs. 4, 5). Most regression equations relating tree age to stem diameter had relatively high scatter (e.g., Pine reach 3, $R^2 = 0.12$), while others had lower scatter (e.g., Pine reach 2, $R^2 = 0.67$). All regressions were significant at $P < 0.05$.

Age and size structure data showed the same trends. On both streams, maximum stem diameter, maximum tree age, and number of age classes increased with elevation (Figs. 6, 7). However, maximum age and size at Bishop Creek was lower at all elevations, particularly for the lowest elevation reach. The maximum age of black cottonwood trees at the high, mid and low elevation reaches at Pine Creek was 129, 113, and 98 years, respectively, compared to 103, 74, and 39 for elevationally matched reaches of Bishop Creek. In all reaches of both streams black cottonwoods were most abundant in the smallest size class (<10-cm dbh; data not shown) and youngest age class (<20 years of age) (Fig. 7).

Mortality. The percentage of standing dead cottonwood trees differed substantially between elevationally matched reaches of Pine and Bishop creeks (Table 1). At Pine Creek, <11% of the mature trees were dead, and most of these had died as a result of beaver (*Castor canadensis*) activity. Within Bishop Creek, the percentage of dead trees within the mature population ranged from 14 to 33% between reaches. Return visits in 1991 revealed additional mortality within some Bishop Creek reaches but not within Pine Creek. Highest mortality was within Bishop Creek reach 4, where 60% of the marked black cottonwood trees had died. Seven percent of the marked trees in Bishop reach 2 had died.

Of the cored dead trees in Bishop Creek reach 2, three were determined to have died during drought periods (1972–1973 and 1976–1977 (Fig. 8) and one during a high-flow year (1982); one tree could not be assigned a year of death. Annual flow volumes during the drought periods ranged from <1 hm^3 to <7 hm^3 . The dead trees grew more slowly in the years prior to death than they did over their lifetime, and on average grew slower than living trees of similar age (Table 2). The dead trees did not have significantly higher annual growth fluctuation than live trees, although the Bishop Creek trees as a group had greater annual growth fluctuation than did Pine Creek

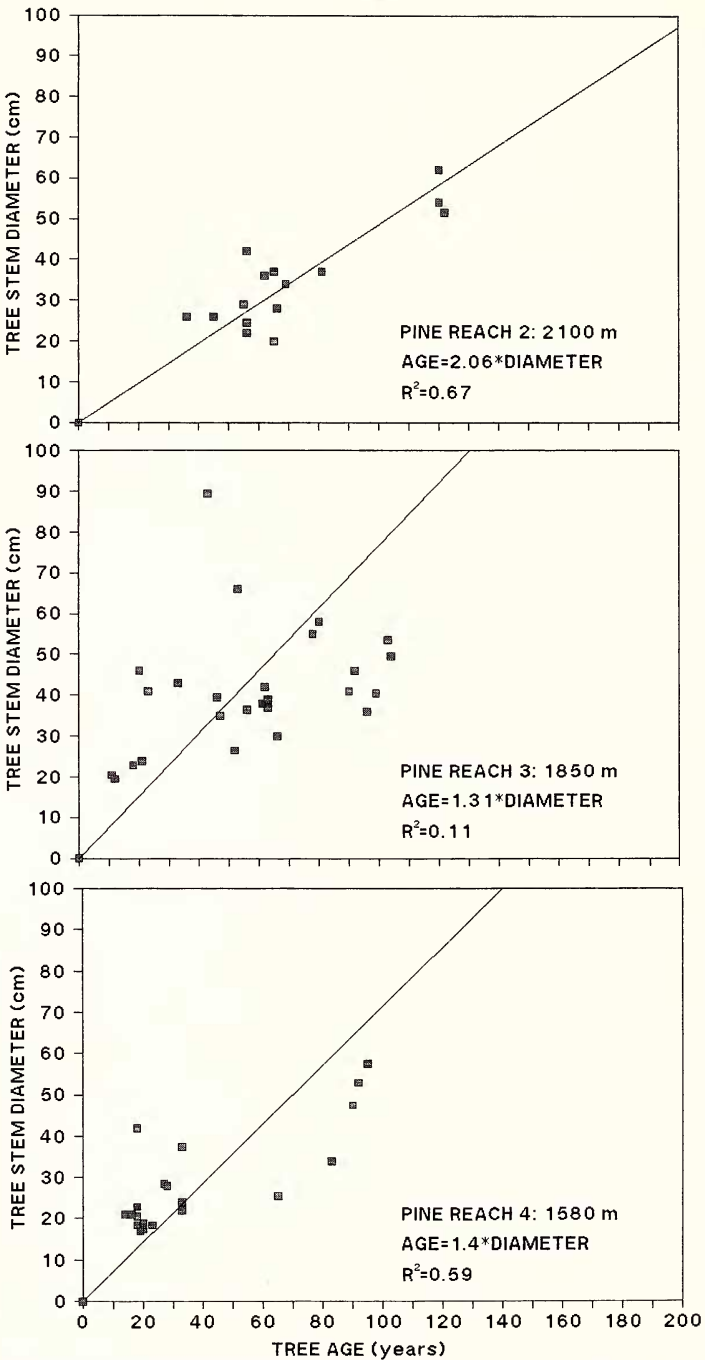


FIG. 4. Size-age plots for *Populus trichocarpa* at Pine Creek, by reach.

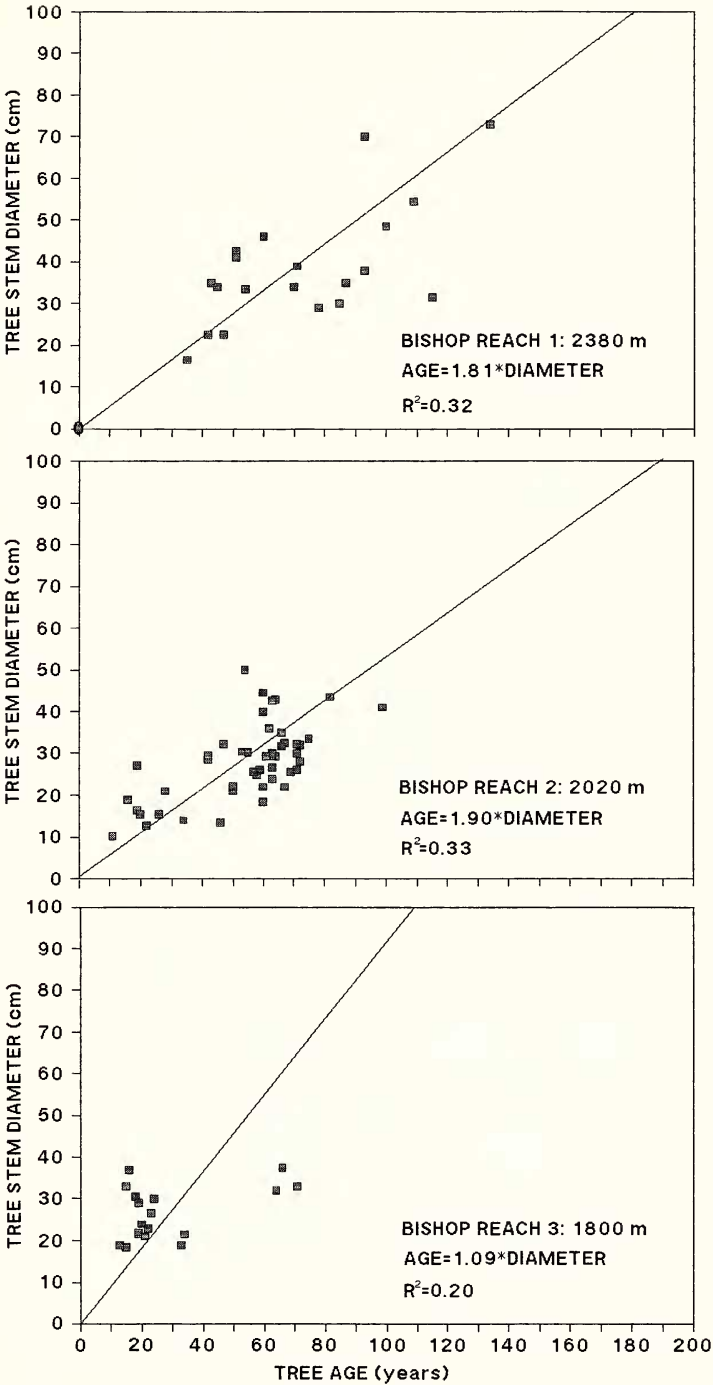


FIG. 5. Size-age plots for *Populus trichocarpa* at Bishop Creek, by reach.

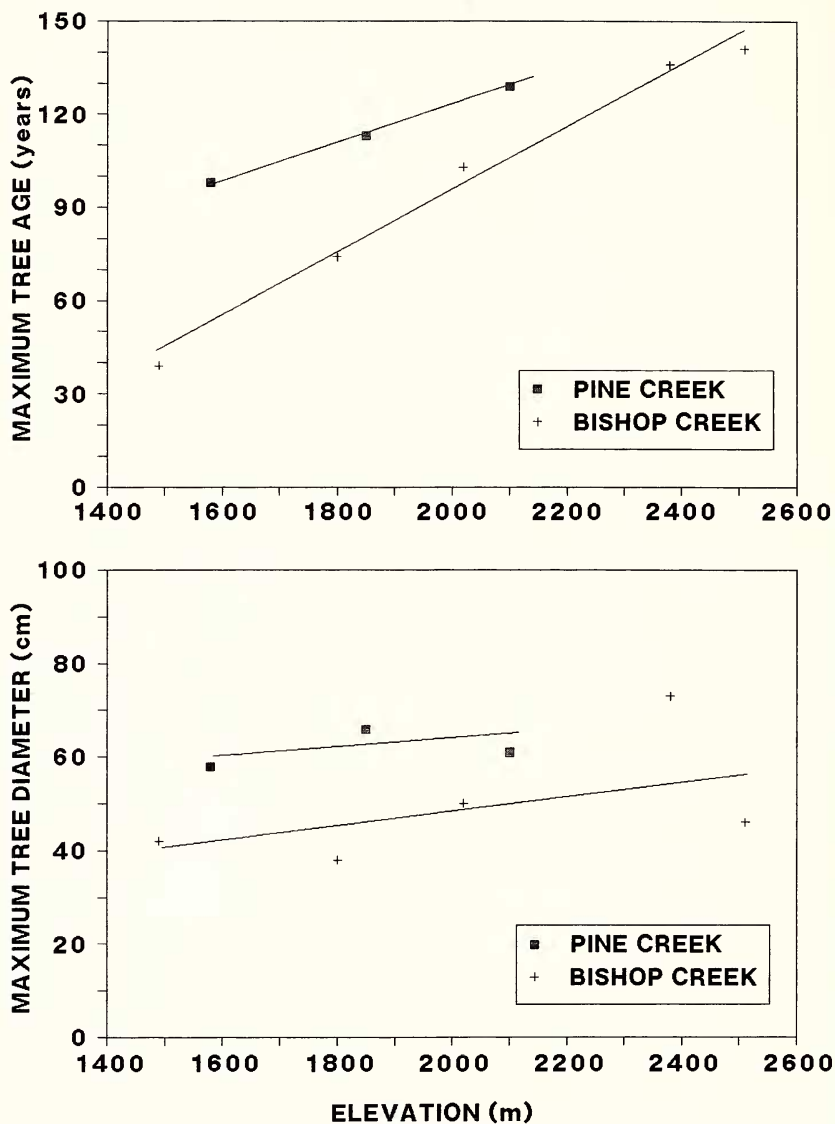


FIG. 6. Maximum size and age of *Populus trichocarpa* at Pine and Bishop creeks, as a function of elevation.

trees ($P < 0.05$; Table 1). The average age of the dead trees (57 ± 11) was somewhat younger than the present age of most of the older cohorts in the reach (60 to 80 years). At the time of their deaths 8 to 17 years ago, the dead trees were among the oldest in the reach. Spatially, the dead black cottonwoods were found near the stream

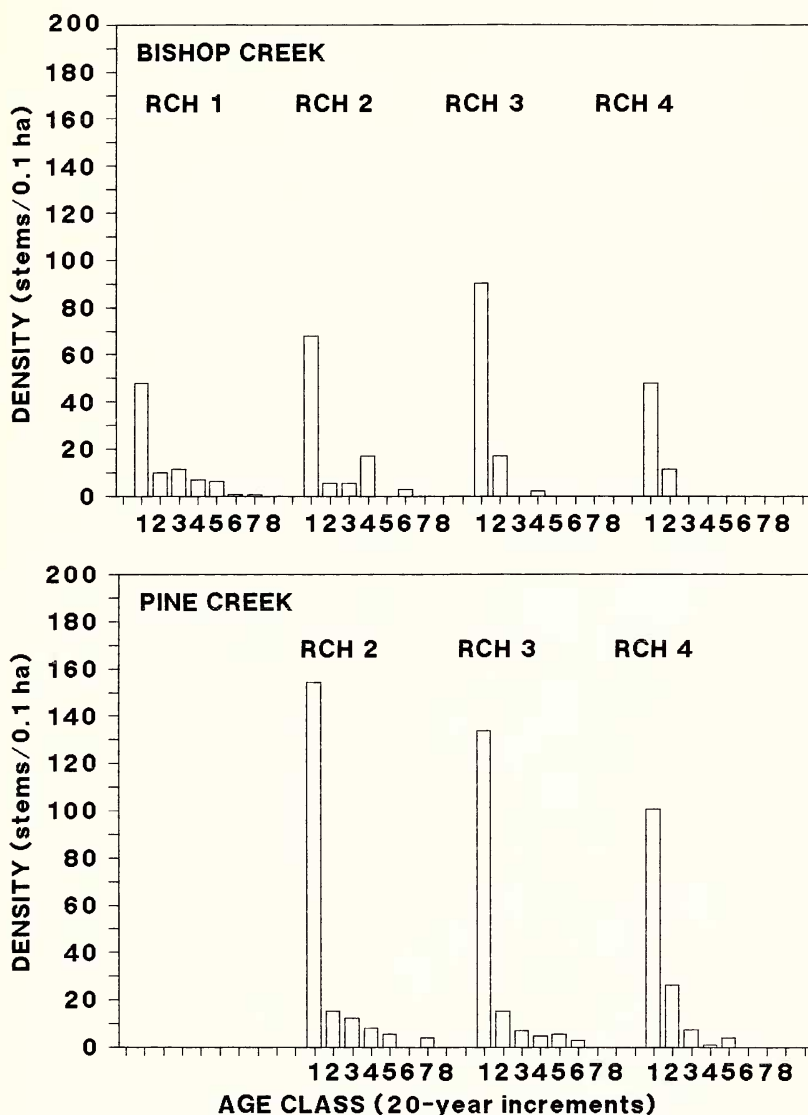


FIG. 7. Age structure of *Populus trichocarpa* at Pine and Bishop creeks, by reach.

edge to the perimeter of the floodplain (up to 20 m from the stream edge).

At Rush Creek, year of death was determined for 9 of 11 dead black cottonwood trees. Of these, 7 died during drought periods (1972–1973 and 1976–1977) (Fig. 8) and 2 died during or immediately after high flow years (1967, 1983). Average age of the dead

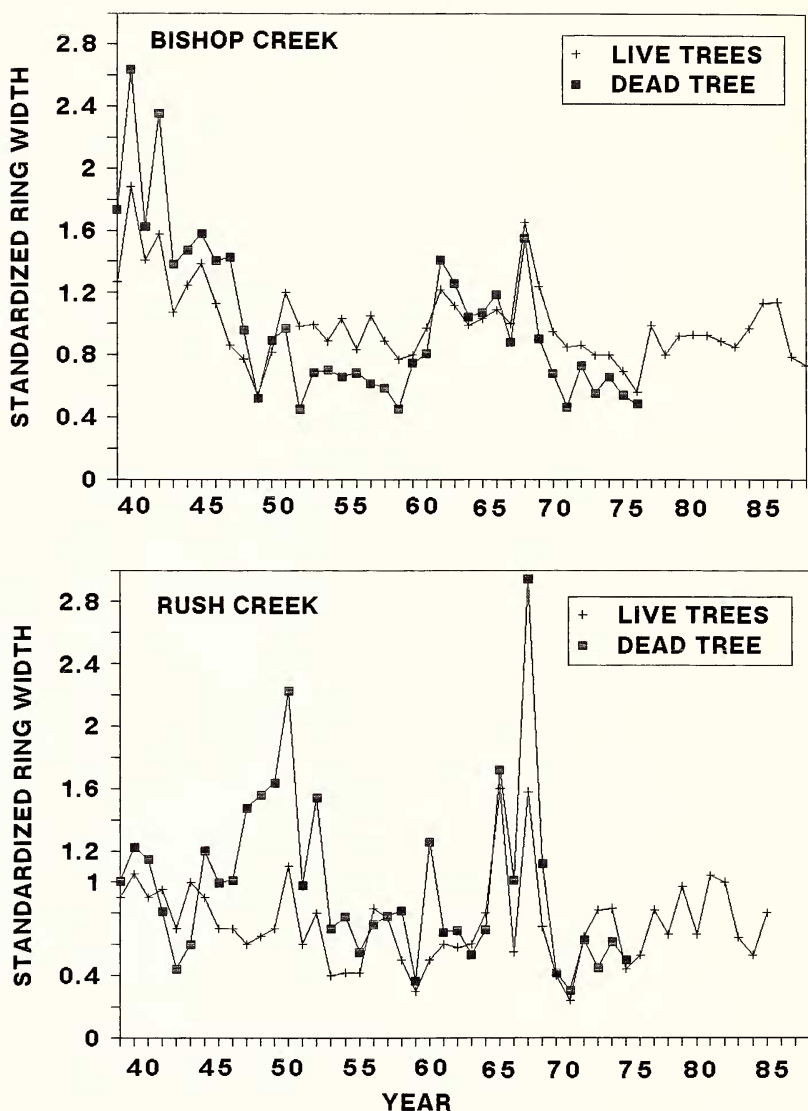


FIG. 8. Ring width chronologies of representative dead *Populus trichocarpa* at Bishop and Rush creeks, overlain on the chronologies of live trees.

trees was 47 ± 9 years. Spatially, the dead trees were present throughout the floodplain, from the streamedge to the floodplain perimeter. Similar to the Bishop Creek trees, recent and lifetime growth rates were lower for dead trees than live trees. Annual growth fluctuation (i.e., mean sensitivity of the tree-ring chronologies) did not differ between dead and live trees at Rush Creek (Table 2).

TABLE 2. RADIAL GROWTH RATE (ANNUAL RING WIDTH) AND EXTENT OF ANNUAL GROWTH VARIATION FOR LIVE AND DEAD *POPULUS TRICHOCARPA* AT BISHOP AND RUSH CREEKS. Growth during the five years prior to tree death is also indicated.

Stream	Status	Sample size	Lifetime growth (mm yr ⁻¹)	Pre-death growth (mm yr ⁻¹)	Annual growth variation ¹
Bishop Creek	Live	20	1.88 ± 0.47	—	35 ± 13
	Dead	5	1.32 ± 0.32	0.46 ± 0.44	39 ± 03
Rush Creek	Live	18	1.85 ± 0.77	—	43 ± 11
	Dead	10	1.65 ± 0.74	1.08 ± 0.81	43 ± 09

¹ Mean sensitivity of the ring chronologies.

DISCUSSION

The data in this study indicate that changes in natural flow regimes have reduced the biological integrity of riparian cottonwood stands along Bishop Creek. Riparian stands differed in dominant species composition between low elevations of Bishop Creek and free-flowing Pine Creek, indicating that extreme stress had resulted in ecosystem-level changes (Taub 1987). Population-level changes indicative of moderate stress were apparent in all stream reaches, including higher elevations where diversion effects were less visually apparent. In comparison to black cottonwood stands along Pine Creek, those along Bishop Creek were younger, had lower tree density, higher tree mortality, and lower canopy foliage density. Tree ring analysis at Bishop Creek and another diverted stream, Rush Creek, suggested that episodic floods and chronic droughts have been at least partly responsible for these biotic changes, by increasing the incidence of cottonwood mortality and preventing trees from living out their natural lifespans.

Floods and droughts are natural phenomena in aridland riparian systems. Floods often are a driving variable in riparian ecosystems, and although they can trigger recruitment events they also can cause tree death by physiologically stressing the trees or physically removing them (Stromberg et al. 1991). Sustained low flows during prolonged natural droughts also cause death of aridland riparian trees (Albertson and Weaver 1945). At Bishop and Rush Creeks, low flow periods have become lower in flow magnitude and longer in duration, because flows are completely diverted from the stream in normal and below normal water years. Extreme events, however, have been little altered. As a result, mortality incidence is high for cottonwoods along the diverted streams, particularly at low elevations. Flood magnitude is known to increase with elevation (Leopold 1964), while drought effects can be increased at low elevations because of high temperature and evaporative demand.

The data in this study specifically implicate the 1982–1983 flood years as mortality years for Bishop Creek cottonwoods. We speculate

that the damaging effects of large floods are high at Bishop Creek and other diverted streams because: (1) reduced base flows have allowed cottonwood establishment in flood-prone near-stream sites; and (2) reductions in vegetative cover arising from flow diversion have decreased the extent of vegetation-related attenuation of flood flows. At Bishop Creek, the restriction of many cottonwoods to a narrow strip (< 5 m) along the streamedge may be a result of diverted streamflow, predisposing the trees to greater impact from flood flows. Although dams and diversions may reduce the frequency of low magnitude flood flows and allow encroachment of trees into the channel (Harris et al. 1987), they do not necessarily eliminate the infrequent large-magnitude flood flows. This may ultimately increase the damage to riparian trees.

Flood-related mortality may be compounded by chronic drought stress, which weakens the resistance of the trees. Drought, however, also independently contributed to cottonwood death at Rush Creek and Bishop Creek. Mortality periods corresponded to drought periods (e.g., early and mid 1970's), which were periods of very low flow release. The present drought period (1987–1991) also correlates with a period of mortality at Bishop Creek. Similar drought-related mortality was not observed at Pine Creek. The trees that died from drought at Bishop and Rush creeks had very low radial growth rates in the years prior to death. Both of these streams have been shown to be “sensitive” rather than “complacent” sites in the sense that growth of cottonwood trees fluctuates with annual flow volume (Stromberg and Patten 1990, 1991). Thus it is not surprising that very low flows reduced growth rates to lethal levels. Besides having low radial growth in the years prior to death, the dead trees also grew more slowly than the population as a whole. We did not attempt to determine whether lower growth rates were a result of genetic factors or environmental factors (e.g., the dead trees may have been growing on drier microsites within the riparian zone). Whatever the cause, lower growth may have rendered the trees more susceptible to extreme hydrological events (e.g., droughts and floods). Greater annual growth fluctuation of the Bishop Creek trees (a result of higher flow fluctuation) also may have increased their susceptibility.

The contributions of juvenile mortality or reduced recruitment to the low canopy foliage density at Bishop Creek were not directly addressed in this study. Other studies have indicated that young cottonwoods are more sensitive to diversion than are mature trees (Smith et al. 1991). The size structure data collected in our study, however, revealed a high relative abundance of saplings. Cottonwood establishment may be facilitated at Bishop Creek by the openness of the canopy (a factor that may stimulate root sprouting), combined with seasonal flow peaks that still follow natural patterns (a factor that would favor seedling recruitment). This contrasts with

the situation at streams such as Rush Creek, where altered seasonal flow peaks (July vs. June) may be preventing sexual seedling recruitment by desynchronizing the periods of flow peaks and seed germination (Fenner et al. 1985; Stromberg and Patten 1989).

MANAGEMENT IMPLICATIONS

Prior studies have indicated that release of a certain average volume of seasonal or annual flow is necessary for maintaining riparian cottonwoods (Stromberg and Patten 1989, 1990). This present study suggests that flow minima and maxima also need to be managed at diverted or regulated streams. Adherence to specific minima and maxima would help to reduce drought-related mortality and to encourage establishment in areas less susceptible to flood damage, and would thus help to restore the biological integrity of the riparian trees.

The following techniques could be used to establish minimum flows. First, the relative difference between mean (or median) flows and minimum annual flows in free-flowing streams in the region could be used as an index. At Pine Creek, for example, the lowest annual flow during the last 20 years was about 2.5 times lower than the mean. By extrapolation, this would mean that low flows should not be less than $5 \text{ hm}^3 \text{ yr}^{-1}$ in the diverted Bishop Creek reaches. This approach is validated by another approach, that being the use of flows during lethal drought periods as an index of insufficient flows. Data in this study suggest that flows $< 5 \text{ hm}^3 \text{ yr}^{-1}$ have been lethal to mature cottonwoods at Bishop Creek. Thus, 5 hm^3 is perhaps a good first approximation of non-lethal flows for this stream. Whatever values are selected, subsequent monitoring of vegetation response should be an integral component of riparian management.

With respect to maximum flows, a prudent approach would be to allow floods to occur with a magnitude, timing, and frequency characteristic of natural flow regimes (Stromberg et al. 1991). At Bishop Creek, for example, the frequency of small floods should be increased while at the same time there should be a decrease in the range between the mean annual flow and the maximum annual flow, as well as between the mean and maximum instantaneous flow. Assuming that maximum flows can not be reduced (due to reservoir constraints), then mean annual flows must be increased. This should reduce flood damage by reducing tree establishment in flood prone sites and increasing vegetative cover that moderates downstream flood effects.

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